Geographical patterns of hoverfly (Diptera, Syrphidae) functional groups in Europe: inconsistency in environmental correlates and latitudinal trends

PETR KEIL[1], FRANK DZIOCK[2] and DAVID STORCH[1,3]

[1]Department of Ecology, Faculty of Science, Charles University, Praha, Czech Republic, [2]Department of Biodiversity Dynamics in Terrestrial Ecosystems, Institute of Ecology, Technische Universität Berlin, Berlin, Germany and [3]Centre for Theoretical Study, Charles University in Prague & Academy of Sciences of the Czech Republic, Praha, Czech Republic

Abstract. 1. Relationships between species richness in higher taxa and large-scale environmental variables have been widely studied over the past 15 years. Much less is known about how different functional groups (FGs) of species with similar biological and life-history traits contribute to the overall trends, or how they differ in species-richness patterns.

2. Multivariate analysis clustered 641 species of Syrphidae into eight FGs on the basis of 10 life-history features, revealing feeding strategy as the main factor separating the groups.

3. Geographical trends in species richness and determinants of species richness within the FGs were compared across Europe.

4. Total species richness showed no latitudinal trend. However, the richness of individual FGs revealed variable relationships with latitude, including positive, negative, and hump-shaped ones. This appeared to be related to how different environmental factors affected species richness within FGs.

5. Functional groups differed in their responses to the environmental variables. Annual temperature, evapotranspiration, and elevation span were the most important variables *separating* the FGs in ordination analysis. The multiple regression models showed further differences between FGs and their responses to the environment.

6. The FG approach revealed important inconsistencies in latitudinal diversity gradients and diversity-climate relationships.

Key words. Europe, environmental correlates, functional groups, latitudinal gradient, species richness, Syrphidae.

Introduction

The past decade has seen much interest in the environmental determinants of patterns of large-scale species richness (Kerr *et al.*, 2001; Hawkins *et al.*, 2003a; Currie *et al.*, 2004). In most cases, the number of species has been used as the response variable, although some studies predict different diversity patterns for organisms differing in their trophic rank (Holt *et al.*, 1999), degree of specialisation (Novotny *et al.*, 2002), range size (Jetz & Rahbek, 2002), body size (Blackburn & Gaston, 1996), ther-

moregulation regime (Allen *et al.*, 2002) or overwintering strategy (Wallisdevries & Van Swaay, 2006). Trans-continental studies have rarely involved comparing correlates of different functional groups (FGs) within a single higher taxon. A FG is defined here as a group of species sharing similar ecological features that can influence their performance in nature.

Current research on environmental correlates of diversity of FGs has been based mostly on observations at local and landscape scales (Davies *et al.*, 2003; Stevens *et al.*, 2003; Schweiger *et al.*, 2007). This work has revealed some interesting phenomena. For example, some relationships between diversity and environment only emerge when a functional approach is employed (Williams & Hero, 2001). Functional groups within a single taxon may have a species richness determined by completely different

factors (Williams & Hero, 2001; Schweiger *et al.*, 2007). This suggests that a functional approach may provide a better base for conservation and applied research (Schweiger *et al.*, 2007).

A taxon suited to the functional approach should have a wide range of ecological traits to allow clear functional groups to be identified. Hoverflies (Diptera: Syrphidae) are considered eminently suitable. They inhabit most terrestrial and many aquatic environments as well as differing considerably in their body sizes and mobility. Furthermore, their larvae show a variety of lifestyles and feeding strategies (Sommaggio, 1999). Most importantly, detailed data on the life history traits of all European species exist in a single comprehensive database, Syrph the Net (Speight & Castella, 2006).

The primary aim of this paper is to explore whether (and how) FGs of Syrphidae differ in their response to latitude and selected environmental variables. Patterns over large regions (countries, administrative provinces) across the whole of Europe are considered, instead of focusing on patterns on a local scale. To our knowledge, this approach has not yet been attempted in the functional context. The FGs correspond to objectively defined (by means of multivariate methods) species clusters, based on their biological traits as proposed by Grime *et al.* (1997) and Blondel (2003). Having identified these groups the following hypotheses are tested:

1 On a regional scale, species richness within FGs should consistently follow the most prominent biodiversity gradient – a decrease towards the poles (Gaston, 2000).
2 Species richness within functional groups should consistently conform to the large-scale correlations between diversity and the environment that are commonly observed in animals. The most widely observed pattern is the correlation of animal biodiversity with energetic aspects of climate (Hawkins & Porter, 2003; Hawkins *et al.*, 2003a; Currie, 2007). More specifically, there have been two particular explanations of this correlation. The first is the *more individuals hypothesis,* which states that regions with higher energetic input have higher primary production and can subsequently support larger populations (Wright, 1983; Clarke & Gaston, 2006). Such an explanation would expect evapotranspiration or a combination of temperature and precipitation to be the main variable(s) explaining diversity patterns. The second energy-based explanation anticipates higher diversity in energy-rich areas because of accelerated physiological processes, higher mutation rates, shorter generation times and in turn, higher speciation rates (Rohde, 1992; Allen *et al.*, 2002). This explanation favours temperature alone as the primary explanatory variable (Storch, 2003). Species richness may also be positively enhanced by heterogeneity of habitats and the number of available niches (Kerr *et al.*, 2001; Hawkins & Porter, 2003; Hawkins *et al.*, 2003a; Currie *et al.*, 2004).

Material and methods

Ten life history variables were used to create the FGs for 641 European species of Syrphidae. Species lists of 38 European administrative regions were used as samples (Fig. 1). Species lists from regions of differing size have already been success-

fully used as sampling units in European studies (Ulrich & Buszko, 2003; Bárcena *et al.*, 2004; Konvicka *et al.*, 2006). Some larger regions were sub-divided into smaller administrative units, in order to increase the number of samples. This was only possible in countries with extensive recorded data (France, Germany and Great Britain). Regions for which reliable species checklists were not available (according to Speight & Castella, 2006) were excluded. The number of species within each functional group was calculated for each region. Regression and ordination analyses were performed to identify environmental correlates of species richness within functional groups.

Functional groups

All 641 species of European Syrphidae were classified using categories assigned to 10 life-history traits (Table 1). The classification procedure is similar to that used by Schweiger *et al.* (2007) who performed an analogous study of hoverfly functional richness on the landscape scale. The life-history traits used to identify FGs in our study were: larval microhabitat, larval food, development length, inundation tolerance, number of generations, migratory status, flight period, body size, and macrohabitat of adults (Table 1). This information was taken from Speight and Castella (2006). Body-size data was taken from Dziock (2006). Species of unknown body size (52 out of 641) were assigned the median value of congeneric species. Each species trait contained several subcategories, for example *larval food* (saprophagous, zoophagous, phytophagous, etc.). These subcategories were assigned a value on a scale of 0–3 (0 represents no affinity of the species to the trait subcategory, 3 represents a high affinity of the species to the subcategory). For a detailed description of this coding method, see Chevenet *et al.* (1994) and Speight and Castella (2006). When appropriate, classification techniques are applied to such data and the importance of each trait for the separation of FGs can be evaluated. Here, multiple correspondence analysis using fuzzy-coded variables (FCA; Chevenet *et al.*, 1994; Speight & Castella, 2006) was used to identify the main gradients in the trait matrix. The number of ordination axes was chosen, based upon the results of the scree test (Cattell, 1966). In our case, four axes were retained for further analysis. These were then used to perform cluster analysis [partitioning around medoids (PAM); Kaufman & Rousseeuw, 1990], on the basis of the species scores on the first four ordination axes of the FCA. In contrast to other clustering techniques, PAM is not hierarchical and introduces an objective criterion of cluster validity called *average silhouette* which reflects the tightness and separation of each cluster (Kaufman & Rousseeuw, 1990). The classification that provided a representatively high value of average silhouette and, at the same time, with meaningful and ecologically interpretable clusters was chosen. These clusters represent objectively defined functional groups (FG) upon which the following analyses were based.

Environmental variables

Many variables have been reported to influence biodiversity over large regions (see introduction and Hawkins *et al.*, 2003a). Initially, 14 environmental variables which described the
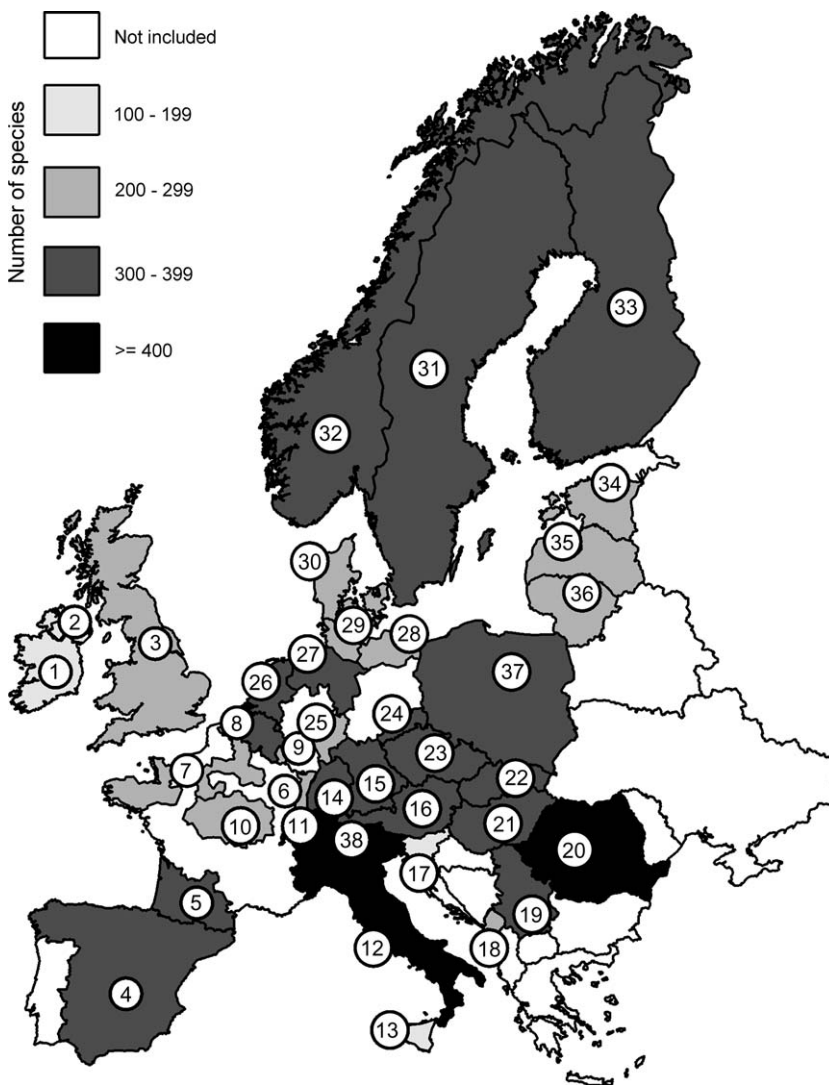
Fig. 1. Total species richness of Syrphidae (Diptera) in 38 European regions used in the analyses. Key: 1: Republic of Ireland, 2: Northern Ireland, 3: Britain (excl. N. Ireland), 4: Spain, 5: South-west France, 6: Alsace-Vosges, 7: North-west France, 8: Belgium, 9: Luxembourg, 10: Central France, 11: Switzerland, 12: Italy, 13: Sicily, 14: Baden-Würtemberg, 15: Bayern, 16: Austria, 17: Slovenia, 18: Montenegro, 19: Serbia, 20: Romania, 21: Hungary, 22: Slovakia, 23: Czech Republic, 24: Sachsen, 25: Hessen, 26: the Netherlands, 27: Nieder-Sachsen & Bremen, 28: Mecklenburg-Vorpommern, 29: Schleswig-Holstein, 30: Denmark, 31: Sweden, 32: Norway, 33: Finland, 34: Estonia, 35: Latvia, 36: Lithuania, 37: Poland, 38: Liechtenstein. For more details see Speight & Castella (2006).

climatic, geographical, topographic and historical conditions were gathered. As a result of inter-correlations between some of the variables, we reduced their number for the purpose of this study. The following variables were used:

1–2 Latitude (°) and longitude (°), estimated for an approximate geographical centre of a region from the atlas by Graves (1995). Note: latitude and longitude should not be considered as real predictors of species richness but as a mere spatial correlate (Hawkins & Diniz-Filho, 2004). That is why we treat latitude separately and do not include it in our environmental models.

3 Area (km^2). This study compares the species richness of regions that differ in size. It is well known that species richness increases with area (Rosenzweig, 1995).

4 Island (logical value 1/0). The species richness of islands decreases with their distance from the mainland (MacArthur & Wilson, 1967). All island regions were excluded, except for Sicily, Great Britain and Ireland. Samples lying on these islands were assigned the logical value 1.

5 Elevation span (m) measured as the difference between the highest and lowest elevation points. This variable has been frequently used as a measure of heterogeneity of habitats and has been reported to explain large-scale variation of species richness (Hawkins & Porter, 2003). Maximum and minimum elevation points were estimated from Graves (1995).

6–7 Mean annual temperature (°C) and mean annual precipitation (mm). National averages were extracted from Mitchell *et al.* (2002). The data are publicly available on http://www.cru.uea.ac.uk/~timm/index.html. In regions where country means were unavailable, data from local meteorological stations (www.meteofrance.com) were averaged.

8 Mean annual actual evapotranspiration – AET (mm/month). This is a measure of water–energy balance or productive potential. This has been frequently used as a surrogate for total primary productivity of an area and has been reported to be an important correlate of species richness in various taxa (Hawkins *et al.*, 2003a). In the current study, AET data from

Table 1. Life history traits used to separate functional groups (FGs) (clusters) of 641 species of European Syrphidae.

Trait variable	Categories (number of fuzzy-coded categories)
Larval microhabitat	Trees, upward climbing lianas, herb layer, timber, dung, litter, stones, nests of social insects, root zone, on/in water plants, submerged sediment/debris, water-saturated ground (12)
Larval food	Saprophagous, saproxylic, phytophagous, zoophagous (4)
Development length (egg-larva-puparium)	Less than 2 months, 2–6 months, 7–12 months, more than 1 year (4)
Inundation tolerance of larva	No inundation tolerance, tolerant with short breathing tube, tolerant with medium-sized breathing tube, tolerant with long breathing tube (4)
Number of generations per year	Less than one, one generation, two generations, more than two (4)
Migratory status	Non-migrating, recorded migrant, strongly migratory (3)
Flight period in Europe	Feburary, March, April, May, June, July, August, September, October, November (10)
Body size	Less than 5, 5–5.9, 6–6.9, 7–7.9, 8–8.9, 9–9.9, 10–11.9, 12–14.9, more than 15 mm (9)
Overwintering phase	Unknown, larva, puparium, adult (4)
Macrohabitat of adults	Forest, open habitat, cultural habitat, wetland, freshwater habitat (5)

Ahn and Tateishi (1994) were averaged (available on http://www.grid.unep.ch/data).

9 Proportion of wetland surface to terrestrial (%). This variable was added to the dataset á posteriori after the initial analyses results, in order to explain some unusual latitudinal trends detected in some FGs (see discussion for more details). The proportion of wetland surface may influence geographical distribution of Syrphidae, as they rarely occur in completely dry conditions (Stubbs & Falk, 2000). The strong right-skew of the distribution, required the variable to be $\log_{10}$ transformed in all analyses. These data were estimated from a map publicly available on UNEP server at http://www.grid.unep.ch/product/publication/freshwater_europe.php. In the case of France, Germany and Italy, wetland data were not available for administrative sub-regions; hence, they were assigned the values of the whole country.

Analysis of diversity-environment correlations

Regression analysis was used to test the influence of environmental variables on (i) total species richness controlled for area and (ii) numbers of species within each functional group controlled for area. The effect of area was controlled for in the following way (for more details see Rosenzweig, 1995): Species-richness data and the area data were both $\log_{10}$ transformed and a straight line was fitted through the transformed data. The area-unbiased species richness (S_A) was then obtained from the residuals as $S_A = 10^{residual\ value}$. Each of the 38 regions (Fig. 1) was treated as a separate sample.

Ordination analysis (Canoco for Windows 4.5; Leps & Smilauer, 2003) was used to explore inconsistencies in species-richness patterns of FGs. The area-corrected numbers of species within a FG were used as the dependent variables (*species* in Canoco terminology). Explanatory environmental variables were the same as in the regression analyses. Forward stepwise selection of variables and a Monte Carlo permutation test ($\alpha = 0.05$ as an inclusion criterion) were used to select the most influential environmental variables and these were used to construct a canonical correspondence analysis (CCA) model (Leps & Smilauer, 2003). The significance of the first two ordination axes was also tested with a Monte Carlo permutation test ($\alpha = 0.05$).

Ordinary least squares regression (OLS) was employed (normal distribution of response variables was assumed) to support the CCA results and to reveal particular predictors of species richness within individual FGs. For selecting among alternative models, traditional significance testing was combined with the information theory approach using the Akaike information criterion corrected for small sample sizes (AIC_c) (Burnham & Anderson, 2002). For each response variable (species richness within functional group), a multiple-regression model was constructed based on successive stepwise addition of the terms. No more than two terms were allowed in each model because of the limited sample sizes ($n = 38$) (Crawley, 2005). In each step the model with the lowest AIC_c value was selected (the difference from other AIC_c values needed to be at least two). Each term was also checked for a non-linear effect (second order polynomial). Additionally, separate effects of all environmental variables were assessed in single-term regressions, testing both for linear effects and for non-linearities revealed by quadratic terms. The residuals of each model were checked for significant spatial autocorrelation (Moran's I) in the first three distance classes. If the residuals were autocorrelated, simultaneous autoregression (SAR in SAM package; Rangel *et al.*, 2006) was performed and the results of SAR and OLS were compared. Geographic distances between samples were used to incorporate the spatial structure into the model.

Results

Ten biological traits were used in the FCA to separate FGs of 641 species of European hoverflies. The strongest correlates of the longest gradient in the trait data (Axis 1) were larval food and inundation tolerance, followed by larval microhabitat and body size (Table 2). The variables with the highest mean correlation ratio (variance of the category scores/total variance) on axes 1–4 were larval food, larval microhabitat, and inundation tolerance followed by the number of generations, development length, body size, and overwintering phase (Table 2). Macrohabitat of

Table 2. Correlation ratios for 10 trait variables along the first four axes of fuzzy correspondence analysis of the trait matrix. Figures in bold show the ratios which are higher than the axis eigenvalue. Mean correlation ratio is arithmetic mean of axes 1–4.

Trait variable	Axis 1	Axis 2	Axis 3	Axis 4	Mean correlation ratio
Larval food	**0.702**	0.215	**0.278**	**0.501**	0.424
Larval microhabitat	**0.551**	0.132	**0.637**	**0.218**	0.385
Inundation tolerance	**0.700**	0.115	0.226	**0.239**	0.32
Number of generations	0.274	**0.534**	**0.277**	0.122	0.302
Development length	0.301	**0.421**	**0.261**	0.073	0.264
Body size	**0.433**	0.096	**0.276**	0.093	0.225
Overwintering phase	0.239	**0.257**	0.001	**0.374**	0.218
Macrohabitat of adults	0.123	0.091	0.212	0.051	0.119
Migratory status	0.003	**0.429**	0.013	0.008	0.113
Flight period	0.009	0.077	0.007	0.024	0.029
Eigenvalues	0.334	0.237	0.219	0.17	

adults, migratory status, and flight period revealed the weakest contribution to the separation of species into the FGs.

Cluster analysis of species scores on the first four ordination axes separated eight ecologically interpretable clusters. It became apparent there was a correspondence between clusters and the trophic strategies of larvae (Table 3). For this reason we named them as follows: SAPRO1, small saprophages with an affinity to water plants and with a medium-sized breathing tube; SAPRO2, large common saprophages inhabiting wet places and dung, with a long breathing tube; SAPROXYL1, saproxylic, univoltine, medium-to-large species; SAPROXYL2, very large saproxylic species with long development and a long breathing tube; SAPROPHYT, mostly medium-sized sapro-phytophages and some zoophages inhabiting lower layers of vegetation; ZOO1, medium-sized aphidophages with intermediate trophic specialisation; ZOO2: small-to-medium generalist zoophages with very short development; typical r-strategists; and PHYTO,

species with phytophagous larvae and the only group overwintering in the pupal stage.

FGs differed in their response to latitude (Fig. 2). Total (area-unbiased) species richness showed no correlation with latitude. A significant decrease in area-unbiased species richness northwards was observed in FGs PHYTO ($r^2 = 0.11$, $P = 0.035$), SAPROPHYT ($r^2 = 0.27$, $P < 0.001$), SAPROXYL2 ($r^2 = 0.16$, $P = 0.012$), and ZOO1 ($r^2 = 0.26$, $P < 0.001$). FGs SAPROXYL1 ($r^2 = 0.24$, $P = 0.076$), SAPRO1 ($r^2 = 0.17$, $P = 0.033$), and SAPRO2 ($r^2 = 0.43$, $P < 0.001$) showed an unimodal response to latitude. In the case of SAPRO2 the modus was located at the very north (59th parallel), demonstrating that the trend seemed to be more of an increase of species richness northwards rather than a unimodal response (Figs 2 and 3). Species richness of functional group ZOO2 showed no significant trend with latitude. Latitudinal model for PHYTO showed autocorrelated residuals and after taking spatial structure into

Table 3. Functional grouping of 641 species of European Syrphidae as obtained from cluster analysis on the basis of species scores on the first four axes of fuzzy correspondence analysis of the species-trait matrix. The clusters were created using partitioning around medoids cluster analyses (functions pam and clara in R, package Cluster), Euclidean distances.

| Functional group abbreviation	N	Larval food	Larval microsite	Inundation tolerance (length of breathing tube)	Generations per year	Develop. Length [months]	Body size [mm]	Overwintering phase
SAPRO1	54	Saprophages	Wet microsites, water plants	Medium	1–2	7–12, some less	5–8	Larva
SAPRO2	52	Saprophages	Wet microsites, dung	High	1–2	2–12	10–15	Larva, adult
SAPROXYL1	63	Saproxylic	Trees, timber, roots	Medium	1	7–12	7–15+	Larva
SAPROXYL2	25	Saproxylic	Trees	High	Less than 1	12+	12–15+	Larva
SAPROPHYT	104	Mostly sapro-phytophages, few zoophages	Herblayer, roots	Mostly none (few with short tube)	1–2	7–12, some less	7–12	Larva
ZOO1	183	Zoophages	Trees, herblayer	None	1–2	7–12	6–12	Larva
ZOO2	55	Zoophages	Trees, herblayer, roots	None	2	2–12, some less	6–12	Larva, adult
PHYTO	105	Phytophages	Herblayer, roots	Mostly none (few with short tube)	1	7–12, some less	6–12	Puparium
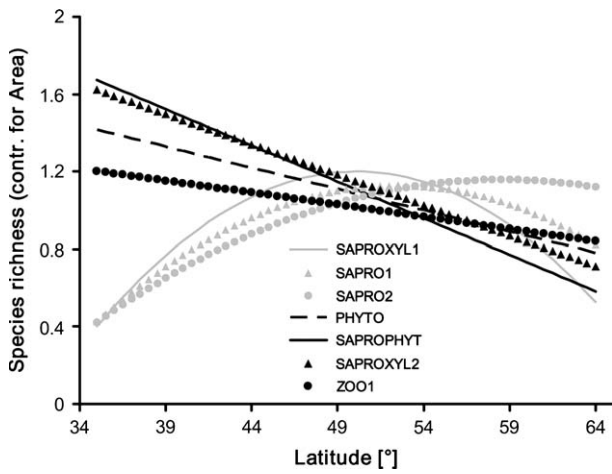
Fig. 2. Latitudinal trends of species richness of seven functional groups of European syrphidae. The trends are represented here by the linear (black) or second order polynomial (grey) model fitted to the species-richness data. The polynomial model was used in case it provided a lower Akaike information criterion corrected for small sample sizes (AIC$_c$) value than the linear model. The total species richness and the species richness within group ZOO2 are not plotted as they did not show a significant latitudinal trend.

Fig. 3. Remarkably inversed latitudinal trend of species richness of functional group SAPRO2 (large saprophagous hoverflies).

account, the latitudinal trend was no longer significant. The remaining models either showed no autocorrelation in their residuals or the trend did not change after the incorporation of the spatial structure into the SAR.

Forward selection of variables in Canoco retained four of the environmental variables as the strongest correlates of differences in species richness between functional groups: AET, elevation span, annual temperature, and position on an island. Those were used for the CCA (Fig. 4). The first axis (27.5% of explained variability, $P = 0.002$) of this model was correlated with AET and elevation span. The second axis (12.1% of explained variability, $P = 0.004$) represented the gradient of temperature conditions combined with position on an island (Fig. 4). There was clear separation of trophic strategies along the first ordination axis (Fig. 4) with saprophagous groups in the very left side of the diagram, plant-associated groups (PHYTO, SAPROPHYT) in the very right side and zoophagous and saproxylic groups in the middle (Fig. 4).

The best multiple regression models are described in Table 4. FGs differed in the combination of variables that were included in the best models. However, these variables showed some consistency in the shape of their effect: island always had a negative effect on species richness (significant for SAPRO1, SAPROXYL1, SAPROXYL2, ZOO2, and total species richness) and the effect of AET was always positive (significant for SAPROXYL2, ZOO1, PHYTO, and SAPROPHYT). Except for SAPROXYL1, annual temperature had a negative effect on species richness (significant for SAPRO2, ZOO2, and PHYTO). Elevation span showed a less consistent effect: convex (SAPRO2, ZOO1) or positive (SAPROPHY and total species richness). Residuals from neither of the best models showed significant spatial autocorrelation.
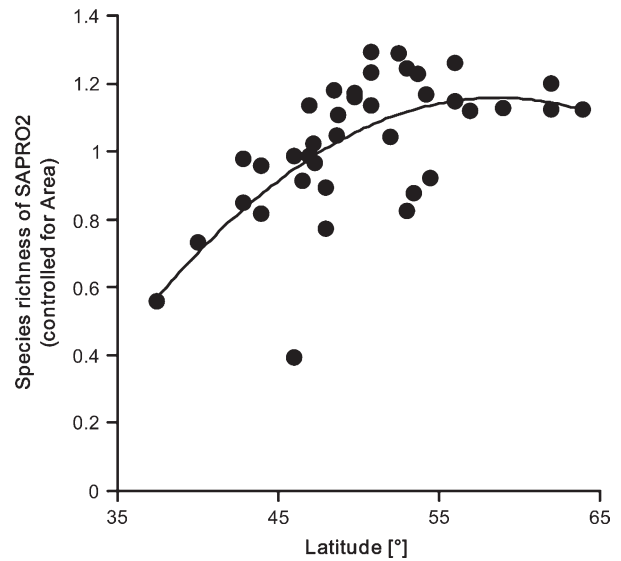
In general, the results of the multiple regression models and the CCA are similar, except for ZOO1. This FG is in fact positively correlated with all of the individual environmental variables used in CCA. This most probably caused the discrepancy between the CCA biplot and the multiple regression model which only uses two environmental variables.
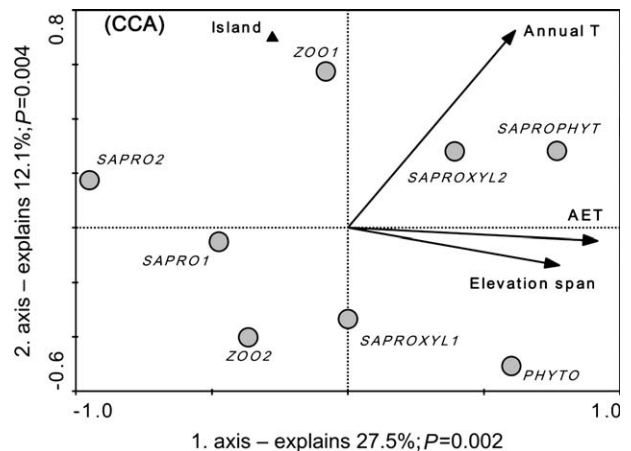

Fig. 4. Canonical correspondence analysis (CCA) plot. Filled circles represent optima of functional groups, arrows are environmental variables and triangles are factors. Axes were constrained by environmental variables selected out by the forward selection and Monte Carlo permutation test. This allowed not only identification of the most important environmental variables responsible for differences in functional composition but also significance testing of these gradients. The effects of actual evapotranspiration (AET) and habitat heterogeneity (elevation span) were inseparable in this model and formed the most important environmental gradient. There was a weaker (but still significant) gradient corresponding with annual temperature and perhaps position on an island.

Table 4. Multiple regression models explaining species richness within functional groups of syrphidae in Europe. The models were selected using stepwise forward selection. AIC$_c$ (akaike information criterion corrected for small sample sizes) was used as model selection criterion. Because of the small number of observations (small sample size) no more than two explanatory variables were allowed in the models. The arrows indicate orientation of the relationships, '↑↓' stand for convex polynomials, '↓↑' for concave polynomials and '–' for negative effect of categorical variables.

Functional group		Model terms	Effect	P	r^2
All species	Complete model	~Island + Elevation span		<0.001	0.41
	Partial effects	Island	(−)	<0.001	0.33
		Elevation span	↑	0.034	0.08
SAPRO1	Complete model	~Island		0.004	0.21
	Partial effects	Island	(−)	0.004	0.21
SAPRO2	Complete model	~Annual T + Elevation span*		<0.001	0.46
	Partial effects	Annual T	↓	<0.001	0.28
		Elevation span*	↓↑	0.0037	0.18
SAPROXYL1	Complete model	~Island + Annual T*		<0.001	0.51
	Partial effects	Island	(−)	<0.001	0.4
		Annual T*	↑↓	0.027	0.11
SAPROXYL2	Complete model	~AET* + Island		<0.001	0.43
	Partial effects	AET*	↑	<0.001	0.31
		Island	(−)	0.008	0.12
ZOO1	Complete model	~AET + Elevation span*		<0.001	0.43
	Partial effects	AET	↑	<0.001	0.32
		Elevation span*	↓↑	0.04	0.11
ZOO2	Complete model	~Island + Annual T		<0.001	0.34
	Partial effects	Island	(−)	<0.001	0.25
		Annual T	↓	0.038	0.09
PHYTO	Complete model	~AET + Annual T		<0.001	0.64
	Partial effects	AET	↑	<0.001	0.35
		Annual T	↓	<0.001	0.29
SAPROPHYT	Complete model	~Elevation span + AET		<0.001	0.45
	Partial effects	Elevation span	↑	0.004	0.35
		AET	↑	0.021	0.1

*Variable entered as a second-degree polynomial.

Discussion

Functional groups

When an objective way of determining interpretable FGs and their environmental correlates was used, relationships emerged which would have remained hidden if only total species richness had been used. The traits most important for the separation of the FGs were larval food and inundation tolerance, followed by larval microhabitat and body size. The diversity of larval feeding styles in Syrphidae is one of the most prominent features of this taxonomic group (Thompson & Rotheray, 1998) so the relevance of this trait is not surprising. Other studies using similar approaches to define FGs in Syrphidae have also identified the high importance of these life history traits, namely larval food and microsite, as well as inundation tolerance (Dziock, 2006; Schweiger *et al.*, 2007). It seems logical that inundation tolerance explains a large amount of variation in studies carried out in floodplains (Castella & Speight, 1996; Dziock, 2006). However, in larger-scale studies like ours and Schweiger *et al.* (2007), inundation tolerance remains one of the most important traits. This reflects the dependence of all syrphid larvae on moist microsite conditions. Virtually none of the syrphid larvae are resistant to dessication and as such, they do not occur in extremely dry conditions (Stubbs & Falk, 2000).

Grouping of species reduces the amount of variance in the dataset and thus leads to more coarse relationships when analysed. However, the great advantage of the functional grouping approach is that the groups can be interpreted in biological terms. This is not the case for functional diversity indices which reduce the complexity into a single figure (e.g. Petchey & Gaston, 2002).

Unusual latitudinal trends

There was a striking absence of the expected northward decrease in total species richness and also in the species richness of small, fast-developing zoophages. In the case of large saprophages, an almost inverse latitudinal trend was found – with an increase in species richness northwards. Species within this group are quite charismatic, large (genera *Eristalis*, *Helophilus*, *Anasimyia*) and they are easy to collect and identify. Therefore, this reversed latitudinal pattern is unlikely to be a result of the lack of information from southern parts of Europe (note that relatively poorly explored regions like Portugal, Greece or some Balkan countries had already been excluded). The relationship is also unlikely to be a result of the influence of outliers either (Fig. 3). Finally, species richness in the southern parts of Europe could somehow be reduced by the presence

of massive geographic barriers – the Alps and Pyrenees. Previous studies on European butterflies (Hawkins & Porter, 2003) and birds (Hawkins *et al.*, 2003b) showed that the Apennine and Iberian peninsulas do not have lower species richness than the areas north of the mountain ranges. Moreover, the Alps and Pyrenees themselves are actually the regions with the highest species richness in Europe (Hawkins & Porter, 2003; Hawkins *et al.*, 2003b). Hence, we are reluctant to consider the presence of major mountain ranges to be the explanation of observed latitudinal trends. Keil and Konvicka (2005) reported similar patterns of local species richness of Syrphidae in Central Europe. We propose the following explanation: large saprophages are mostly restricted to water during their development. Large relative surfaces of water may support larger populations which are less prone to extinction. This may subsequently cause higher species richness in areas with more wetlands. Species richness of large saprophages indeed correlates with the relative surface of wetlands ($r^2 = 0.16$, $P = 0.012$). Although our measure of wetland surface explains considerably less variation than latitude ($r^2 = 0.43$, $P < 0.001$), we attribute this to the relative inaccuracy of the variable.

Reversed latitudinal gradients have been reported for several taxonomic groups, such as parasitic wasps or aphids (Kindlmann *et al.*, 2007). The fact that a large proportion of the family Syrphidae feeds on aphids and/or mimics Hymenoptera may lead to various speculations. It would be tempting to claim that some hoverflies are another exception from the positive latitude/diversity relationship. However, more detailed research needs to be carried out to test this hypothesis, probably based on grid-based distribution atlases and a study in other continents and spatial scales (at least for large saprophages).

This study is not the first to detect differences in latitudinal gradients between FGs. Bárcena *et al.* (2004) detected two, opposing latitudinal trends between aestival and resident species of European water birds, within the overall trend of a slight decrease of diversity southwards. Thus, the absence of any significant latitudinal gradient in total species richness can be caused by various directions of latitudinal gradients within FGs. These directions can differ and, after they are averaged, may result in a weak or even an undetectable latitudinal gradient of total species richness.

Consistency in responses to environment

Environmental variables that described the availability of energy (AET, annual temperature) and habitat heterogeneity (elevation span) were, in general, the most important variables influencing species richness in functional groups, as shown by the CCA (Fig. 4). However, responses of individual FGs to these variables were not consistent. FGs are reported to vary in response to environmental variables at both the local and landscape scales (Williams & Hero, 2001; Lassau *et al.*, 2005; Schweiger *et al.*, 2007). This variation is usually interpreted in terms of specific environmental requirements of species from different FGs (Lassau *et al.*, 2005). The pattern has scarcely been studied on a macro-scale with broad regional units used as samples. In fact, it has only been the study of Bárcena *et al.*

(2004) that has been carried out on a spatial scale similar to our study. Bárcena *et al.* (2004) found that different FGs of birds had different environmental correlates of species richness. Together with our results, this suggests that the life-history features specific for FGs influence the observable patterns of species richness even on the macro-scale. This is contrary to the traditional macroecological view that on the macro-scale the differences between species are no longer important, and some general patterns emerge (Lawton, 1999). It also contrasts the hypothesis of Currie (2007), in which global patterns of species richness are similar for various organisms and that they are formed primarily by the energetic aspects of climate (Currie, 2007).

Here follows the discussion of particular species richness patterns that were detected within FGs in our study.

For the large saprophages (SAPRO2) and the generalist zoophagous species (ZOO2) the distinct correlation with temperature conditions could be associated with overwintering. As hoverflies overwinter in January, most often in the larval stage, we may hypothesise that their distribution is dictated by the ability of larvae to survive harsh winter conditions. Strong freeze tolerance is known for the generalist aphidophagous species *Syrphus ribesii* (Hart & Bale, 1997a), but the overwintering ability of *Episyrphus balteatus* which has the same feeding mode, but overwinters as an adult, is strongly limited by its restricted cold-hardiness (Hart & Bale, 1997b). The strong negative correlation of functional group ZOO2 with annual temperature would suggest that there are more species with restricted cold-hardiness in this group (larvae or adults) and that freeze-tolerant species represent an exceptional state.

Overwintering behaviour may also explain the vulnerability of FG PHYTO to low temperatures, especially in winter. The majority of hoverflies overwinter in the larval stage, whereas FG PHYTO species overwinter in the pupal stage, making them potentially more sensitive to cold temperatures. Mortality of the phytophagous species of the genus Cheilosia, which are known to overwinter in the pupal stage, has experimentally been shown to increase with lower overwintering temperatures (Gao *et al.*, 1993). In contrast to temperature, actual evapotranspiration had a continuous positive effect on species richness of four FGs. Actual evapotranspiration reflects the precipitation-temperature balance in a region. As hoverfly larvae are generally vulnerable to desiccation, it is unsurprising that species richness is enhanced by a precipitation–temperature balance rather than temperature on its own. However, it is indeed difficult to disentangle the temperature effect and the precipitation effect in a correlative study.

The two plant-inhabiting FGs (PHYTO and SAPROPHYT) were positively associated with elevation span, even after accounting for spatial autocorrelation. This variable is considered to reflect heterogeneity of suitable habitats in a region. The species richness of specialist plant-inhabiting species is usually influenced more by habitat heterogeneity than the species richness of generalist species (Warren *et al.*, 2001). Habitat heterogeneity has been highlighted as having strong potential to explain species richness gradients (Kerr *et al.*, 2001), and the association between plant and animal diversities has been widely reported (Siemann *et al.*, 1998). Therefore, the association found by the current study is not surprising, although the

plant–animal correlations have rarely been observed on such large spatial scales (Hawkins & Porter, 2003; Hawkins & Pausas, 2004).

Final remarks

As a result of the low number of available regional checklists in Europe, the results have to be treated with caution for several reasons.

Sampling effort differs between the regions, ranging from more than 500 000 records (United Kingdom) to far lower numbers of records, for example in Slovenia. Also neither land use intensity, nor land use history were included in the analysis, despite the knowledge that hoverflies are strongly affected by past land use (Schweiger *et al.*, 2007). The relatively impoverished fauna of some regions (e.g. the U.K. and some parts of Germany) may well be caused by high-intensity land use. Despite these limitations, significant exceptions to general biogeographic rules were unveiled, such as the inverse or nearly inversed latitudinal trends, or the deviations from the well-established climate-diversity relationship (Currie, 2007) and those exceptions are, at least in some cases, not caused by data inadequacy.

A more detailed and grid-based extension of this study should be done as soon as European-wide grid-based data for hoverflies are available. Grid data are already available for the U.K. and the Netherlands (Biesmeijer *et al.*, 2006), and there are strong efforts to compile such data for Germany. However, many southern European regions are far from being in this situation. Therefore, the studies exploring species-richness patterns of hoverflies across the whole Europe are, for the time being, possible only when national species lists are used as samples.

Finally, it is now time to undertake further analyses of large-scale species-richness data using FG approaches in order to understand macroecological patterns correctly.

Acknowledgements

References

Ahn, C.-H. & Tateishi, R. (1994) Development of a global 30-minute grid potential evapotranspiration dataset. *Journal of Japan Society of Photogrammetry and Remote Sensing*, **33**, 12–21.

Allen, A.P., Brown, J.H. & Gillooly, J.F. (2002) Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science*, **297**, 1545–1548.

Bárcena, S., Real, R., Olivero, J. & Vargas, J.M. (2004) Latitudinal trends in breeding waterbird species richness in Europe and their environmental correlates. *Biodiversity and Conservation*, **13**, 1997–2014.

Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemuller, R., Edwards, M., Peeters, T. *et al.* (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science*, **313**, 351–354.

Blackburn, T.M. & Gaston, K.J. (1996) Spatial patterns in the body sizes of bird species in the New World. *Oikos*, **77**, 436–446.

Blondel, J. (2003) Guilds or functional groups: does it matter? *Oikos*, **100**, 223–231.

Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference – A Practical Information-Theoretic Approach*. Springer-Verlag, New York.

Castella, E. & Speight, M.C.D. (1996) Knowledge representation using fuzzy coded variables: an example based on the use of Syrphidae (Insecta, Diptera) in the assessment of riverine wetlands. *Ecological Modelling*, **85**, 13–25.

Cattell, R.B. (1966) The scree test for the number of factors. *Multivariate Behavioral Research*, **1**, 245–276.

Chevenet, F., Doledec, S. & Chessel, D. (1994) A fuzzy coding approach for the analysis of long-term ecological data. *Freshwater Biology*, **31**, 295–309.

Clarke, A. & Gaston, K.J. (2006) Climate, energy and diversity. *Proceedings of the Royal Society B-Biological Sciences*, **273**, 2257–2266.

Crawley, M.J. (2005) *Statistical Computing – An Introduction to Data Analysis using S-Plus*. John Wiley & Sons, Chichester, U.K.

Currie, D.J. (2007). Regional-to-global patterns of biodiversity, and what they have to say about mechanisms. *Scaling Biodiversity* (ed. by D. Storch, P. A. Marquet and J. H. Brown), pp. 258–282. Cambridge University Press, Cambridge, U.K.

Currie, D.J., Mittelbach, G.G., Cornell, H.V., Field, R., Guegan, J.F., Hawkins, B.A. *et al.* (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, **7**, 1121–1134.

Davies, R.G., Eggleton, P., Jones, D.T., Gathorne-Hardy, F.J. & Hernandez, L.M. (2003) Evolution of termite functional diversity: analysis and synthesis of local ecological and regional influences on local species richness. *Journal of Biogeography*, **30**, 847–877.

Dziock, F. (2006) Life-history data in bioindication procedures, using the example of hoverflies (Diptera: Syrphidae) in the Elbe floodplain. *International Review of Hydrobiology*, **91**, 341–363.

Gao, J.F., Zhang, G.X., Qin, Y.C., Yu, K., Li, M.H. & Qin, Y. (1993) Field survey on the overwintering of syrphids in Changbai mountains, and experiments on artificial protection of the overwintering syrphid flies. *Chinese Journal of Biological Control*, **9**, 142–143.

Gaston, K.J. (2000) Global patterns in biodiversity. *Nature*, **405**, 220–227.

Graves, W. (1995) *National Geographic Atlas of the World*. National Geographic Society, Washington, District of Columbia.

Grime, J.P., Thompson, K., Hunt, R., Hodgson, J.G., Cornelissen, J.H.C., Rorison, I.H. *et al.* (1997) Integrated screening validates primary axes of specialisation in plants. *Oikos*, **79**, 259–281.

Hart, A.J. & Bale, J.S. (1997a) Evidence for the first strongly freeze-tolerant insect found in the U.K. *Ecological Entomology*, **22**, 242–245.

Hart, A.J. & Bale, J.S. (1997b) Cold tolerance of the aphid predator *Episyrphus balteatus* (DeGeer) (Diptera, Syrphidae). *Physiological Entomology*, **22**, 332–338.

Hawkins, B.A. & Diniz-Filho, J.A.F. (2004) 'Latitude' and geographic patterns in species richness. *Ecography*, **27**, 268–272.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guegan, J.F., Kaufman, D.M. *et al.* (2003a) Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, **84**, 3105–3117.

Hawkins, B.A. & Pausas, J.G. (2004) Does plant richness influence animal richness? the mammals of Catalonia (NE Spain). *Diversity and Distributions*, **10**, 247–252.

Hawkins, B.A. & Porter, E.E. (2003) Water-energy balance and the geographic pattern of species richness of western Palearctic butterflies. *Ecological Entomology*, **28**, 678–686.

Hawkins, B.A., Porter, E.E. & Diniz-Filho, J.A.F. (2003b) Productivity and history as predictors of the latitudinal diversity gradient of terrestrial birds. *Ecology*, **84**, 1608–1623.

Holt, R.D., Lawton, J.H., Polis, G.A. & Martinez, N.D. (1999) Trophic rank and the species-area relationship. *Ecology*, **80**, 1495–1504.

Jetz, W. & Rahbek, C. (2002) Geographic range size and determinants of avian species richness. *Science*, **297**, 1548–1551.

Kaufman, L. & Rousseeuw, P.J. (1990) *Finding Groups in Data: An Introduction to Cluster Analysis*. John Wiley & Sons, New York.

Keil, P. & Konvicka, M. (2005) Local species richness of Central European hoverflies (Diptera: Syrphidae): a lesson taught by local faunal lists. *Diversity and Distributions*, **11**, 417–426.

Kerr, J.T., Southwood, T.R.E. & Cihlar, J. (2001) Remotely sensed habitat diversity predicts butterfly species richness and community similarity in Canada. *Proceedings of the National Academy of Sciences of the United States of America*, **98**, 11365–11370.

Kindlmann, P., Schödelbauerová, I. & Dixon, A.F.G. (2007) Inverse latitudinal gradients in species diversity. *Scaling Biodiversity* (ed. by D. Storch, P. A. Marquet and J. H. Brown), pp. 246–257. Cambridge University Press, Cambridge, U.K.

Konvicka, M., Fric, Z. & Benes, J. (2006) Butterfly extinctions in European states: do socioeconomic conditions matter more than physical geography? *Global Ecology and Biogeography*, **15**, 82–92.

Lassau, S.A., Hochuli, D.F., Cassis, G. & Reid, C.A.M. (2005) Effects of habitat complexity on forest beetle diversity: do functional groups respond consistently? *Diversity and Distributions*, **11**, 73–82.

Lawton, J.H. (1999) Are there general laws in ecology? *Oikos*, **84**, 177–192.

Leps, J. & Smilauer, P. (2003) *Multivariate Analysis of Ecological Data using CANOCO*. Cambridge University Press, Cambridge, U.K.

MacArthur, R.H. & Wilson, E.O. (1967) *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey.

Mitchell, T.D., Hulme, M. & New, M. (2002) Climate data for political areas. *Area*, **34**, 109–112.

Novotny, V., Basset, Y., Miller, S.E., Weiblen, G.D., Bremer, B., Cizek, L. *et al.* (2002) Low host specificity of herbivorous insects in a tropical forest. *Nature*, **416**, 841–844.

Petchey, O.L. & Gaston, K.J. (2002) Functional diversity (FD), species richness and community composition. *Ecology Letters*, **5**, 402–411.

Rangel, T., Diniz-Filho, J.A.F. & Bini, L.M. (2006) Towards an integrated computational tool for spatial analysis in macroecology and biogeography. *Global Ecology and Biogeography*, **15**, 321–327.

Rohde, K. (1992) Latitudinal gradients in species-diversity – the search for the primary cause. *Oikos*, **65**, 514–527.

Rosenzweig, M.L. (1995) *Species Diversity in Space and Time*. Cambridge University Press, Cambridge, U.K.

Schweiger, O., Musche, M., Bailey, D., Billeter, R., Diekotter, T., Hendrickx, F. *et al.* (2007) Functional richness of local hoverfly communities (Diptera, Syrphidae) in response to land use across temperate Europe. *Oikos*, **116**, 461–472.

Siemann, E., Tilman, D., Haarstad, J. & Ritchie, M. (1998) Experimental tests of the dependence of arthropod diversity on plant diversity. *American Naturalist*, **152**, 738–750.

Sommaggio, D. (1999) Syrphidae: can they be used as environmental bioindicators? *Agriculture Ecosystems & Environment*, **74**, 343–356.

Speight, M.C.D. & Castella, E. (2006) StN database: content and glossary of terms, Ferrara, 2006. *Syrph the Net, the Database of European Syrphidae* (ed. by M. C. D. Speight, E. Castella, J.-P. Sarthou and C. Monteil), pp. 77. Syrph the Net publications, Dublin, Ireland.

Stevens, R.D., Cox, S.B., Strauss, R.E. & Willig, M.R. (2003) Patterns of functional diversity across an extensive environmental gradient: vertebrate consumers, hidden treatments and latitudinal trends. *Ecology Letters*, **6**, 1099–1108.

Storch, D. (2003) Comment on "Global biodiversity, biochemical kinetics, and the energetic-equivalence rule". *Science*, **299**, 346b.

Stubbs, A.E. & Falk, S.J. (2000) *British Hoverflies – An Illustrated Identification Guide.* British Entomological and Natural History Society, Reading, Pennsylvania.

Thompson, F.C. & Rotheray, G. (1998). Family Syrphidae. *Contributions to a Manual of Palaearctic Diptera (with Special Reference to Flies of Economic Importance) Vol. 3, Higher Brachycera* (ed. by L. Papp and B. Darvas), pp. 81–139. Science Herald, Budapest, Hungary.

Ulrich, W. & Buszko, J. (2003) Species-area relationships of butterflies in Europe and species richness forecasting. *Ecography*, **26**, 365–373.

Wallisdevries, M.F. & Van Swaay, C.A.M. (2006) Global warming and excess nitrogen may induce butterfly decline by microclimatic cooling. *Global Change Biology*, **12**, 1620–1626.

Warren, M.S., Hill, J.K., Thomas, J.A., Asher, J., Fox, R., Huntley, B. *et al.* (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, **414**, 65–69.

Williams, S.E. & Hero, J.M. (2001) Multiple determinants of Australian tropical frog biodiversity. *Biological Conservation*, **98**, 1–10.

Wright, D.H. (1983) Species-energy theory: an extension of species-area theory. *Oikos*, **41**, 496–506.